THE WOOD OF AMENTOTAXUS

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CONTROVERSY OVER THE TAXONOMIC relationship of the Taxineae with the Coniferineae has created a new interest in the field of wood anatomy. This has been reflected by the flurry of investigations being conducted in families such as the Podocarpaceae.

The systematic position of *Amentotaxus* is somewhat uncertain (see Keng, 1969). While many authors place *Amentotaxus* in the Taxaceae, this genus has also been referred to the Cephalotaxaceae or even considered to represent a separate family, the Amentotaxaceae. When Kudo and Yamamoto (1931) described this last family, it was considered to be represented by only a single species, *Amentotaxus argotaenia* (Hance) Pilger. In his revision of *Amentotaxus* Li (1952) recognized four species. However, the description and publication of three new species of *Amentotaxus* based on leaf morphology would appear to have been overly optimistic and has not gone unchallenged. Hu (1964) recognized only three of the species, since she thought that *Amentotaxus cathayensis* Li could not be usefully upheld as distinct. Moreover, Chuang and Hu (1963) considered that *Amentotaxus formosana* Li was better referred to *Amentotaxus argotaenia* (Hance) Pilger. The divergence of opinion has increased the need to investigate any anatomical features that may be of taxonomic importance. In connection with this work it was thought an examination of the wood anatomy would be worthwhile, even though taxonomic evaluation at the subgeneric level is not often successful in this field. A comparative study of the wood anatomy within the genus *Amentotaxus* is considerably limited by the lack of availability of suitable material; most locations of *Amentotaxus* are in China. The scanty and now somewhat rare wood specimens were collected before 1935, with the exception of some from Taiwan.

PRIOR INVESTIGATIONS

Tang (1933) gave a short description of *Amentotaxus argotaenia*, based on two specimens from the province of Kwangtung in China. He noted rays 1–4 cells high in one specimen whereas in the other they were mostly 3–5 cells high. He also mentioned a slight difference in tracheid wall thickness between the early and late wood. A shorter description was made by Prince (1938). He stated in his introduction to the Taxineae that crassulae are clearly developed. Phillips' (1948) brief description mentioned that the horizontal walls of the ray cells are relatively thick and sparsely pitted; and that the parenchyma cells are wider than the tracheids and have nodular end walls.

The description given by Greguss (1955), based on wood from Taiwan, was much more detailed. According to Greguss the tracheid wall thickness in early wood is not significantly different from that of the late wood. He did not mention the presence of crassulae. Bordered pits are absent or rare on the tangential walls of tracheids, but on the radial wall they form one irregular row. Spiral thickenings are mostly paired. The pit aperture, which is rounded to slit-shaped, is very often enclosed by a pair of spirals and lies in the same direction as the spiral. Aperture direction was given as mostly 45° to the axis. There was no reference to ray wall thickness, but Greguss regarded the end wall as generally smooth. His more detailed description of the axial parenchyma is in agreement with Phillips'.

PRESENT DESCRIPTIONS

Amentotaxus argotaenia (Hance) Pilger (*A. formosana* Li). Uw 18635.

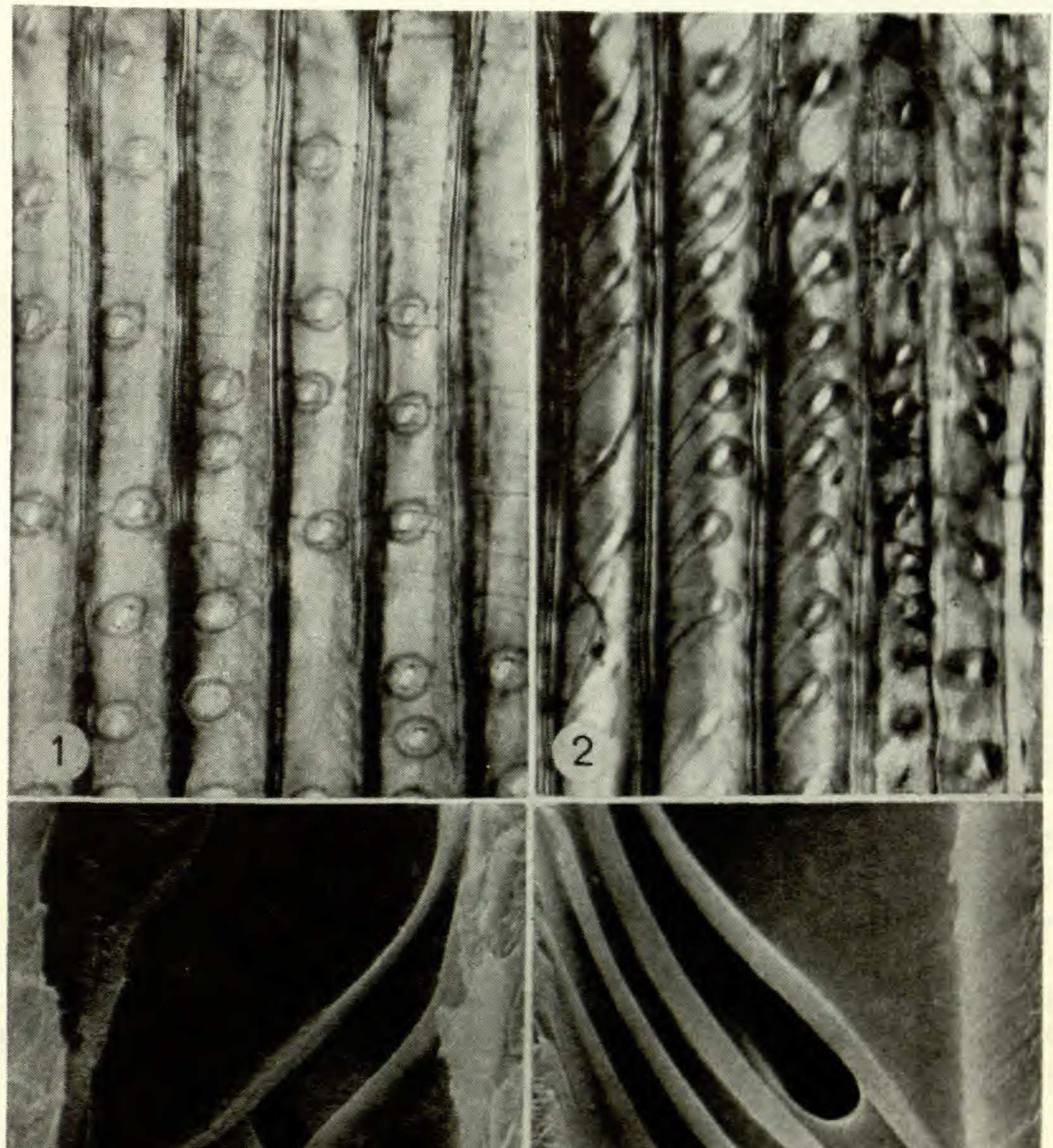
LOCATION: Taiwan (Formosa). Obtained from the Institute of Forest Botany, University of Tokyo, Japan. No.: TOFOw *5721*.

COLLECTOR: Dr. *Ryozo Kanehira*.

A smooth textured wood with a yellow-brown color. The growth rings although distinct are not so pronounced as in the Gymnosperms of the temperate zones. Their width varies from 40 to more than 90 cells. There is a gradual transition from early to late wood, and the late wood consists of only (2)4–5 rows of flattened tracheids.

The *tracheids* are rounded or angular in transverse section and display intercellular spaces. A few tracheids are present with a loosening of the secondary wall. Double spiral bands, 3–6 μ wide, appear to be characteristic of this wood. They vary in angle from almost horizontal (FIGURE 1), mostly in the early wood, to up to 60° (FIGURE 2), mostly in the late wood. Crassulae are present. The bordered pits are without torus and are rare on the tangential walls; on the radial walls they are arranged mostly in one irregular row but occasionally partially biseriate rows are found. Their size varies from 12–15 μ in the early wood, to 10–16 μ in the late wood. The pit apertures lie within the double spiral bands and are oval to lenticular, particularly in the late wood. In the early wood the aperture is oriented almost perpendicularly to the spiral bands (FIGURE 3) and mostly parallel to the bands (FIGURE 4) in the late tracheids. The aperture sizes vary from 2–5 $\mu \times$ 5–10 μ in the early wood to 2–4 $\mu \times$ 4–12 μ in the late wood. Pits are frequently accompanied by checking, which is more apparent in the late wood.

Tracheid measurements — in early wood: (17)25–30(40) μ radial and (17)28–32(40) μ tangential; in late wood: 10–14 μ radial, (15)25–28(35) μ tangential. Length: 800–3000 μ, average 2080 μ. The wall thickness is not significantly different in early and late wood and ranges from 2.5–5 μ.



FIGURES 1–4, *Amentotaxus argotaenia.* 1, Radial section showing horizontal spiral bands, × 280. 2, Radial section showing spiral bands up to 60°, × 280. 3, Radial section showing apertures perpendicular to spiral bands, × 1920. 4, Radial section showing apertures parallel to bands, × 2000. [FIGURES 3 and 4 S. E. M.]

The *wood rays* are uniseriate or occasionally partially two cells wide. This does not appear to represent a truly biseriate state, for occasionally in the transverse section, the end walls of ray cells are seen to meet diagonally. This point when viewed in the tangential section may give the impression of a biseriate ray. Rays are composed of parenchyma cells only with no ray tracheids, although thin-walled marginal ray parenchyma without cross-field pitting is frequently seen (FIGURE 5). Cupressoid cross-field pitting; 1–2 pits per cross-field, occasionally 3–4 pits, which, when found, are seen only in the outer row of pitted cells. In the early wood the largest pits are: 6–8 μ, aperture 5–6 μ; in the late wood: 7–10 μ and 5–8 μ respectively. The pits between ray and axial parenchyma are simple, 7–10 μ, though larger irregular pits up to 25 μ are present. There is occasional pitting in the horizontal walls and thin patches are also seen, probably from a fungal infection; mycelia were found throughout the specimen. Although the horizontal walls are generally smooth, they are very uneven in thickness. The end walls are thin and smooth, not nodular, and often join the horizontal walls obliquely. Indentures are present. Number of rays per mm.^{2} 50–60. Width of rays cells 12–18 μ, height 20–30 μ. The rays generally 1–3, maximum 11 cells high (275 μ). Distribution frequency — number of cells high and percent (in parentheses): 1 (21); 2 (43); 3 (23); 4 (8); 5 (3); 6+ (2).

Parenchyma is relatively abundant in the early wood, the distribution being diffuse but with a tendency to form small groups and short tangential bands (FIGURE 6). In the late wood it is scarce. The cells are mostly empty. The diameter of the cells varies from 20–50 μ but is generally 30–45 μ. The end walls are pitted and mostly nodular (FIGURE 7). The pits of the vertical walls are rounded or oval, 3–10 μ wide, although irregular pitting is common together with a tendency to form large irregular pits up to 25 μ wide.

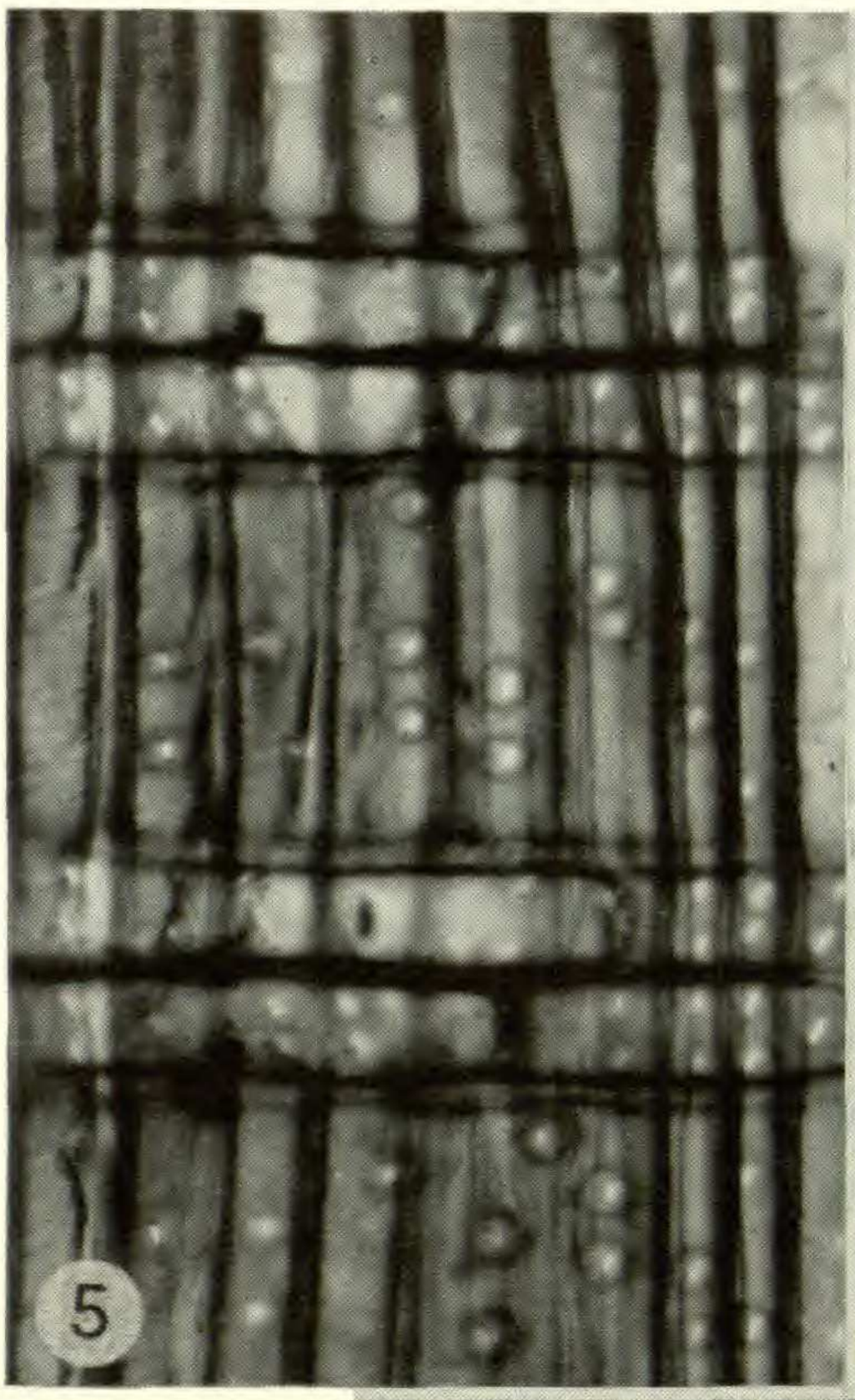
Amentotaxus argotaenia (Hance) Pilger (*A. formosana* Li). Uw 18638.

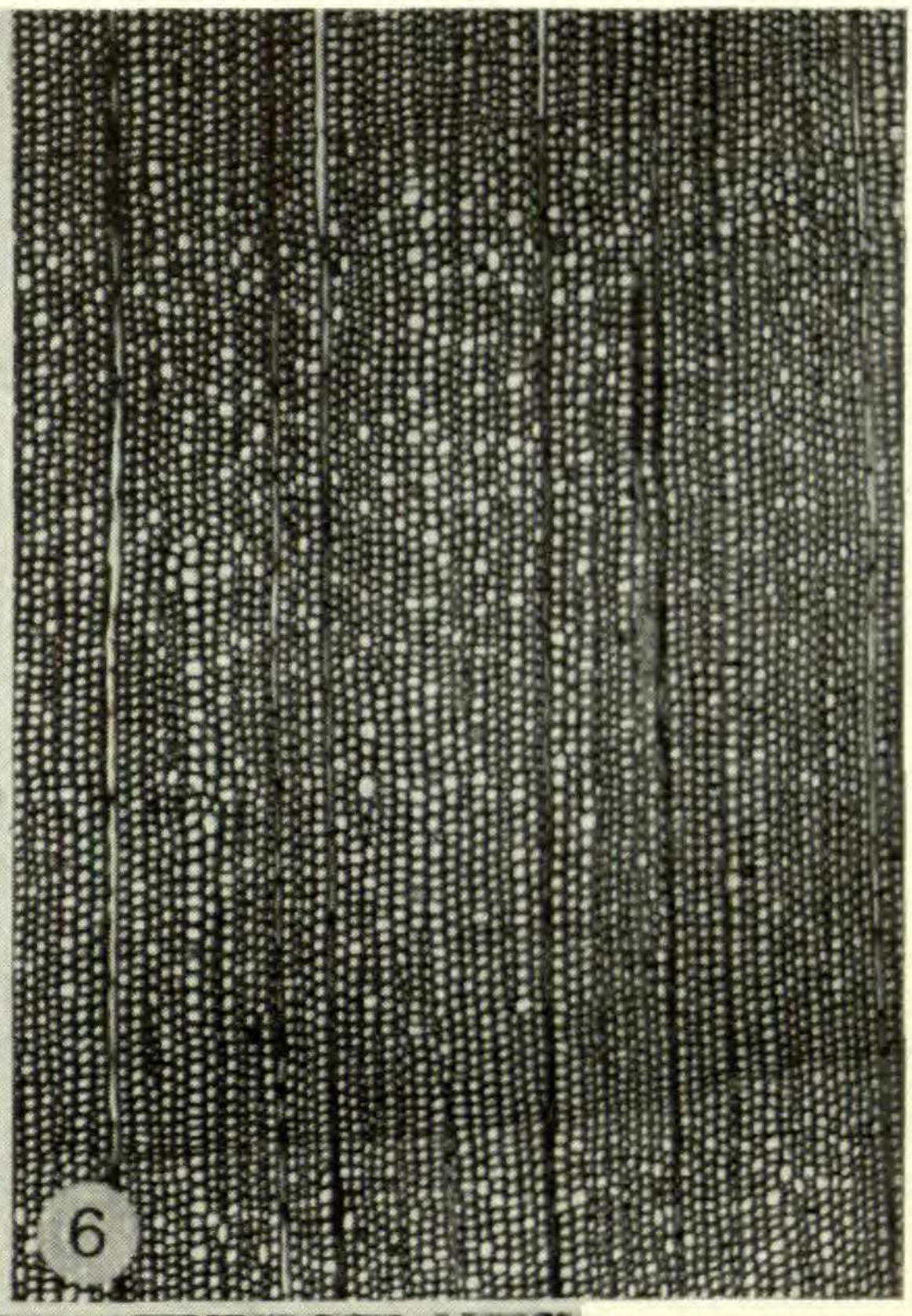
LOCATION: Taiwan (Formosa). Obtained from the U.S. Forest Products Laboratory, Madison, Wisc. No. *9369*. Originally from Dr. *Ryozo Kanehira*.

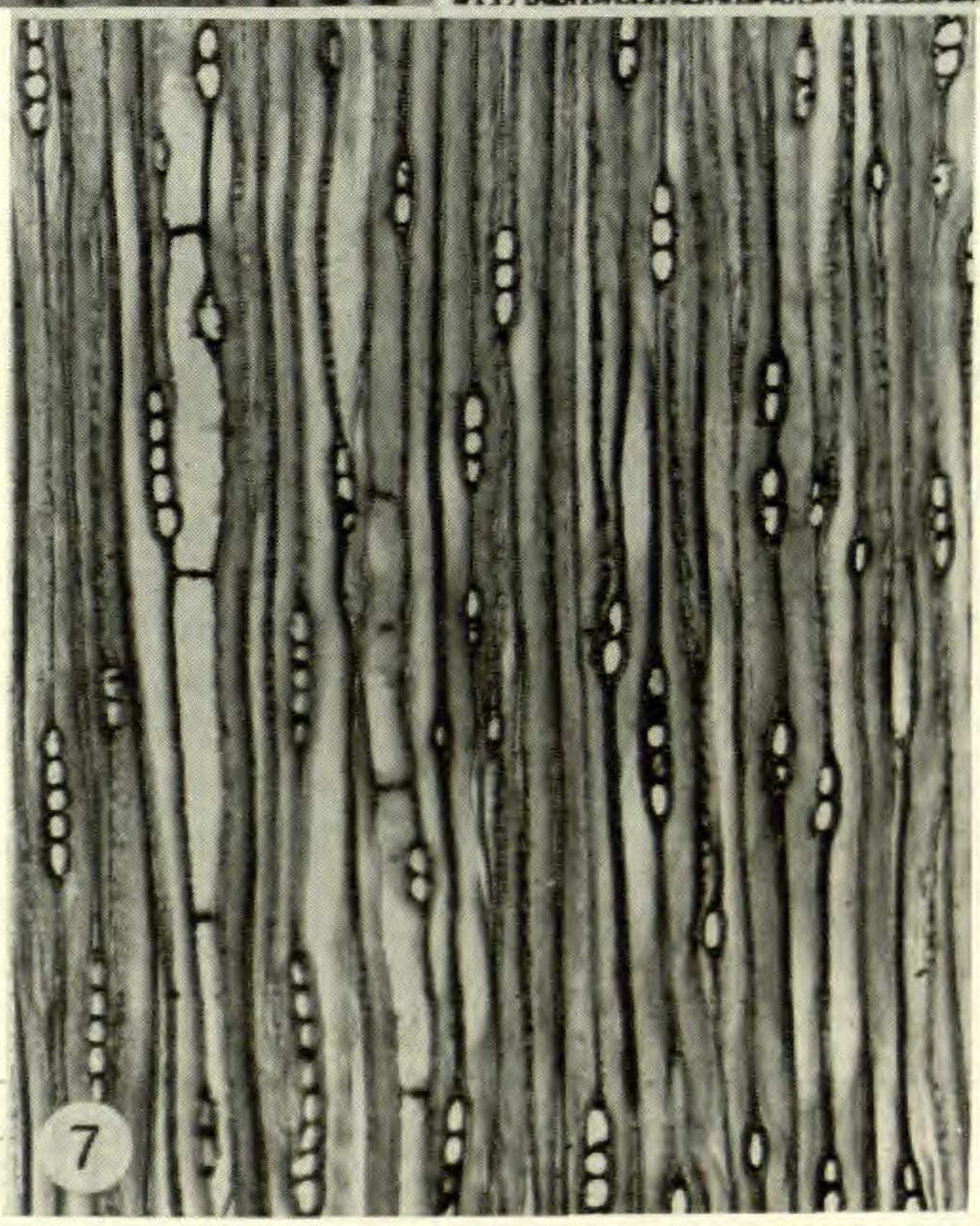
In this specimen the growth rings vary from 20–70 cells wide. The late wood consists of 2–4(5) flattened tracheids. The double spiral band is mostly horizontal, but occasionally up to 30°, 45° is rare. Tracheid lengths are 850–2650 μ with an average of 1900 μ. The rays are generally 1–4, maximum 12 cells high (275 μ). Distribution frequency — number of cells high and percent (in parentheses): 1 (26); 2 (42); 3 (11); 4 (14); 5 (4); 6+ (3). The parenchyma has a diameter of (15)25–40(50) μ, with pits of diameter 4–8 μ and irregular pits up to 30 μ wide

Amentotaxus argotaenia (Hance) Pilger, *sensu stricto*. Uw 18636.

LOCATION: listed as unknown, but believed to be Kwangtung. Obtained from the Institute of Forest Botany, University of Tokyo, Japan.







FIGURES 5–7. *Amentotaxus argotaenia*. 5, Radial section showing thin-walled marginal ray parenchyma, × 160. 6, Transverse section illustrating parenchyma in small groups and short tangential bands, × 30. 7, Tangential section showing general ray distribution and demonstrating axial ray parenchyma with nodular end walls, × 70.

No.: TOFOw *10848*. Collector unknown, but received from Dr. Y. Tang of China in 1935.

The description is comparable to that of Uw 18635, with the following modifications: the growth rings have a width of between 35–70 cells. The late wood consists of 2–3(4) rows of flattened tracheids. The angle of the double spiral bands ranges between 30° and 60°, but mostly 45°. Tracheid lengths vary from 1300–2600 μ, averaging 1890 μ. The parenchyma cells of the rays, although smooth, are slightly thicker, 0.5–1 μ, than in Uw 18635. Number of rays per mm.^{2} 30–40. Rays are generally 1–4, maximum 13 cells high (300 μ). Distribution frequency — number of cells high and percent (in parentheses): 1 (10); 2 (31); 3 (23); 4 (16); 5 (10); 6+ (10).

Parenchyma distribution is similar to Uw 18635, the diameter being (15)25–40(50) μ. The size of the pits is 4–10 μ with irregular pitting and a tendency to form large pits up to 30 μ wide.

Owing to the described variations and the limited number of wood specimens of *Amentotaxus* available, information was obtained from macerations prepared from twig material originating from herbarium specimens. See TABLE 1.

TABLE 1.

TAXA ACCORDING TO LI'S CLASSIFICATION	TRACHEID LENGTH μ	TYPE I* BANDS WITH PITS ORIENTED	TYPE II** BANDS PITS USUALLY PARALLEL	PROPORTION I TO II
1. A. ARGOTAENIA	900–1300	90°–45°	present	I > II
2. A. ARGOTAENIA	750–1050	Mostly 45°	present, more lenticular	I = II
3. A. CATHAYENSIS	600–1200	90°–45°	present, more lenticular	I » II
4. A. FORMOSANA	800–1100	Mostly 45°	present, more lenticular	I = II
5. *A. FORMOSANA	750–1400	More 45° than 90°	present	I < II
6. A. YUNNANENSIS	550–1200	90°–45° slightly lenticular	present, more lenticular	I < II
7. A. YUNNANENSIS	650–1500	90°–45° slightly lenticular	present, more lenticular	I < II

* Type I bands — those double spirals lying horizontal or nearly horizontal.
** Type II bands — those double spirals lying at approximately 45°, pit apertures usually being parallel.

In TABLE 1, **A. formosana* was 4 to 5 years old, and demonstrated the following characteristics: tracheids with bordered pits occurring on the tangential walls but rare; pits on the radial walls forming one row which

is more or less regular; the diameter of the pit borders as much as 25 μ in the early wood; crassulae present.

Rays are uniseriate and consist of parenchyma cells only. Marginal ray parenchyma is not apparent. The horizontal walls are slightly uneven in thickness with occasional pits. Indentures are present but rare. The end walls often join the horizontal walls obliquely. Mostly 2 pits per cross-field but 3–4 pits per cross-field are more frequent than in the wood specimens previously seen. Number of rays per mm.^{2} 100–200. Width of ray cells 8–16 μ, height 20–35 μ. The rays are generally 1–2, maximum 7 cells high (200 μ). Distribution frequency — number of cells high and percent (in parentheses): 1 (65); 2 (27); 3 (6); 4+ (2). The wood parenchyma is relatively abundant in the early wood. The pits are 5–10 μ wide, round and regular. There was no evidence of fungus in this specimen.

DISCUSSION

Obvious anatomical features such as the abundance and arrangement of the wood parenchyma and the double spirals of the tracheids enclosing the bordered pits are of importance at the generic level. Greguss went so far as to say that the arrangement and width of the parenchyma is so characteristic that this genus is immediately distinguishable from all other "conifers." Crassulae which occur in all specimens, including twig material, would appear to be a feature of importance at a higher taxonomic level (Prince, 1938).

The slight variations in tracheid wall thickness are not significant. Their diameter agrees closely with measurements made by Greguss. The tracheid lengths are slightly variable but there is an overlap between the three specimens. Their relative shortness in the twig specimens is in accordance with the first part of one of Sanio's Laws (1872), which states, "In the stem (and branches) the tracheids show an increase in size from within outwards, throughout a number of annual rings." The second part of the rule, ". . . until a certain size is reached, which remains constant in subsequent years," was in dispute; it has been discussed by many authors including Liang (1948) and was reviewed by Dinwoodie (1961). The orientation of the pit apertures within the double spiral might at first sight appear to be of some significance. Further investigations on the herbarium material show a complete range of variation without any apparent pattern. However, where bands lie at about 45°, the somewhat lenticular pits are mostly parallel to the axis of the band. On this point the present author is in agreement with Greguss.

The differences in the cell wall thickness of the rays is slight. Its true thickness is masked by a degree of irregularity, particularly marked in the stem woods. The marginal ray parenchyma described in Araucariaceae and Podocarpaceae (Greguss 1957), was not reported by Greguss (1955) for *Amentotaxus*. It was found in all the stem woods but was not apparent in the twig wood, indicating a later development. In specimen Uw

18636 there are only 30–40 rays per mm.^{2} compared to 50–60 rays per mm.^{2} in the other two. In this same specimen there is also a slight difference in the ray distribution frequency. Tang (1933) noted that one of his specimens had rays 1–4 cells high and the other 3–5 cells high. Differences of this nature would not appear to be of any systematic significance, since measurements on twig material show a marked increase in the number of rays (100–200 per mm.^{2}) and a concurrent decrease in the mean number of cells in each ray. These differences are probably related to factors of age, growth, environment, and other physiological factors.

The width of the axial parenchyma appears to be relatively constant. The only difference seen is in the wall where large irregular pits occur. In twig wood, only regular pits of normal size are found. The presence of a fungal infection could explain the irregularities, as the twig wood appears to be free from fungus. This could also account for the increased irregularity in the thickness in the horizontal walls of the ray parenchyma to be found in the stem wood.

CONCLUSIONS

Amentotaxus is unique at the generic level with the following characteristic features: abundance and distribution of wood parenchyma, nodular end walls; double spiral thickenings of tracheids mostly enclosing pit apertures; rays 1–4 cells high, horizontal walls of uneven thickness with end walls joining at an oblique angle. Some authors, e.g. Kudo and Yamamoto (1931), and Li (1963), have placed *Amentotaxus* in a separate family. On the basis of this investigation into the wood characteristics of *Amentotaxus*, it would be inadvisable for the present author to make any such taxonomic decisions until an adequate comparison has been made with the woods of related genera.

Significant differences are not apparent in the anatomical features of the material examined. It would therefore appear that a) taxonomic evaluation is not possible at the specific level, or b) *Amentotaxus* is monotypic. Should fresh material become available, however, complete with authenticated information about locality, environment, and age of specimen, reinvestigation might be advisable.

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MATERIAL STUDIED (in TABLE 1)

1. *Amentotaxus argotaenia* (Hance) Pilger. HONG KONG: *A. B. Westland s.n.* April 1885 (B).
2. *Amentotaxus argotaenia* (Hance) Pilger. Kwantung, CHINA: *Y. W. Taam 551* (A).
3. *Amentotaxus cathayensis* Li. Western Hupeh, CHINA: *E. H. Wilson 1894* (*K*).
4. *Amentotaxus formosana* Li. TAIWAN: *R. Kanehira & S. Sasaki s.n.* 19 Feb. 1925 (TI).
5. *Amentotaxus formosana* Li. TAIWAN: *R. Kanehira s.n.* 27 Dec. 1925 (A).
6. *Amentotaxus yunnanensis* Li. Yunnan, CHINA: *K. M. Feng 12792* (A).
7. *Amentotaxus yunnanensis* Li. Yunnan, CHINA: *H. T. Tsai 51887* (C, isotype).

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